

Functional losses in ground spider communities due to habitat structure degradation under tropical land-use change

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Abstract. Deforestation and land-use change in tropical regions result in habitat loss and extinction of species that are unable to adapt to the conditions in agricultural landscapes. If the associated loss of functional diversity is not compensated by species colonizing the converted habitats, extinctions might be followed by a reduction or loss of ecosystem functions including biological control. To date, little is known about how land-use change in the tropics alters the functional diversity of invertebrate predators and which key environmental factors may mitigate the decline in functional diversity and predation in litter and soil communities. We applied litter sieving and heat extraction to study ground spider communities and assessed structural characteristics of vegetation and parameters of litter in rainforest and agricultural land-use systems (jungle rubber, rubber, and oil palm monocultures) in a Southeast Asian hotspot of rainforest conversion: Sumatra, Indonesia. We found that (1) spider density, species richness, functional diversity, and community predation (energy flux to spiders) were reduced by 57–98% from rainforest to oil palm monoculture; (2) jungle rubber and rubber monoculture sustained relatively high diversity and predation in ground spiders, but small cryptic spider species strongly declined; (3) high species turnover compensated losses of some functional trait combinations, but did not compensate for the overall loss of functional diversity and predation per unit area; (4) spider diversity was related to habitat structure such as amount of litter, understory density, and understory height, while spider predation was better explained by plant diversity. Management practices that increase habitat-structural complexity and plant diversity such as mulching, reduced weeding, and intercropping monocultures with other plants may contribute to maintaining functional diversity of and predation services provided by ground invertebrate communities in plantations.

Key words: Araneae; belowground biodiversity; energy flux; functional diversity; land-use change; oil palm; predation; rainforest; rubber.

INTRODUCTION

Global deforestation and agricultural intensification are causing strong environmental changes in tropical

regions (Gibbs et al. 2010). These changes are driven primarily by increasing demand in agricultural products, such as palm oil and rubber (Corley and Tinker 2016, Clough et al. 2016). Recent land-use change is particularly prominent in Indonesia, which has experienced the strongest oil palm expansion and is among the leaders in the global chart of deforestation rates (Margono et al. 2014, Corley and Tinker 2016, FAOSTAT 2016). Deforestation and agricultural expansion in tropical regions is

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associated with a decline in taxonomic diversity (Fitzherbert et al. 2008, Drescher et al. 2016) and in the performance of many ecosystem functions (Dislich et al. 2017). Predation is among the key ecosystem functions that decline in agricultural landscapes, leading to a potential weakening of natural pest control (Tscharntke et al. 2005, Gurr et al. 2017). The effect of tropical land-use change on predation has been studied mostly for vertebrate predators that control populations of large-sized insects, but only a few studies have focused on invertebrate predators that control small-sized litter and soil fauna (Barnes et al. 2014, Klarner et al. 2017, Potapov et al. 2019).

The relationship between the loss of taxonomic diversity and ecosystem functions can be disentangled with functional traits, i.e., characteristics of individuals that are relevant to their role in ecosystems and govern their response to environmental changes (Vandewalle et al. 2010, Gagic et al. 2015). Trait-based indices, such as functional diversity and functional redundancy, provide proxies for overall changes in ecosystem functioning and resilience (Mason et al. 2005, Laliberté and Legendre 2010). Land-use change may result in the loss of species, which cannot adapt or colonize plantations rapidly enough and this may be followed by the loss of functional traits and thereby the functional roles these species play. The loss of ecosystem functions thus depends on both the functional redundancy of the original community and the magnitude of species loss (Flynn et al. 2009). If the original community has many functionally redundant species, random species loss may initially have only little effect on functional diversity. However, if there is a factor acting nonrandomly in respect to functional traits (or if functional redundancy of the original community is low), functional diversity may be lost at a rate that equals or even exceeds species loss (Flynn et al. 2009). These different scenarios result in a minor or prominent decrease in ecosystem functioning, respectively. On the other hand, plantations are colonized by new species, which replace some species that were lost. Such species turnover may compensate for the loss of ecosystem functions, or at least maintain the overall level of functional diversity (Aslan et al. 2014, García et al. 2014). To date, very little is known about the rate of species vs. trait loss and turnover in invertebrate communities facing land-use change (Rigal et al. 2018).

Litter and soil harbor about 50% of animal biomass globally (Fierer et al. 2009), which comprises diverse invertebrate communities that form complex food webs, contributing to nutrient cycling and stability of terrestrial ecosystems (Bardgett and van der Putten 2014). In contrast to relatively well-studied effects of tropical land use on aboveground biota, only few community-level studies addressed these effects in litter and soil (Foster et al. 2011). Oil palm and rubber plantations are characterized by a reduction in the amount and nutritional quality of litter (Krashevskaya et al. 2015),

higher pH (Krashevskaya et al. 2015, Allen et al. 2016), lower plant diversity, but higher density of understory compared to rainforest sites (Rembold et al. 2017). These complex changes result in a distinctly different habitat structure, suggesting potential turnover of species and functional traits in soil communities between these different land-use systems (Turner and Foster 2009). It is not clear if this community change can sustain the predation function typically provided by pristine ecosystems. A number of studies found abundance and species richness in litter and soil arthropods to be lower in oil palm plantations compared to rainforest (Chung et al. 2000, Fayle et al. 2010, Barnes et al. 2014), but selected groups of decomposers, such as woodlice and earthworms, may have higher density in monoculture plantations (Hassall et al. 2006, Turner and Foster 2009, Potapov et al. 2019). Due to large body size, however, increased earthworm populations in plantations contribute little energy to higher trophic levels of the invertebrate food web (Potapov et al. 2019). Such differential responses of various animal taxa imply selective exclusion and/or decline of species. This raises questions on which functional traits contribute to the resilience against habitat change (Larsen et al. 2005), which abiotic and biotic factors drive these changes and how differential responses affect the ecosystem service of predation provided by tropical invertebrate predator communities.

Predators with a high flexibility may persist under tropical land-use change, maintaining their abundance (e.g., centipedes; Klarner et al. 2017), but little is known about other major groups of predators such as spiders, despite their importance for ecosystem functioning (Nyffeler and Birkhofer 2017). With more than 48,000 described species (World Spider Catalog; *available online*),¹⁴ spiders (Araneae) are among the most diverse and abundant invertebrate predator taxa worldwide (Wise 1995, Nyffeler and Birkhofer 2017). Different groups of spiders are adapted to specific microhabitats characterized by differences in food availability, vegetation structure and moisture, and employing diverse hunting strategies to target a wide array of prey species (Wise 1995). Spiders span several orders of magnitude in body mass, thus consuming prey of a wide size range (Herberstein 2011). The diversity and versatility of spiders make them play a significant role in terrestrial food webs and render them exceptionally suitable for analyzing changes in predation as a major ecosystem function affected by disturbance (Prieto-Benítez and Méndez 2011, Nyffeler and Birkhofer 2017).

Here, we investigated changes in abundance, diversity, energy flux to spiders (as a proxy for predation), and species and functional trait composition in ground-associated spider communities across sites in tropical rainforest (as reference), rubber agroforest ("jungle rubber")

¹⁴ <https://wsc.nmbe.ch>

and monocultures of rubber and oil palm (as intensively managed agroecosystems). We applied two sampling methods, litter sieving (LS) and heat extraction (HE), to gain a comprehensive understanding of land-use-driven changes in the spider communities. We focused on three research questions: (1) How pronounced is the effect of rainforest conversion into plantations on spider density, species richness, functional diversity, and energy flux to spiders? (2) Does land-use change differentially affect species with different functional traits and which environmental factors drive these effects? (3) What is the relative rate of species and functional trait loss and turnover with land-use change?

METHODS

Study sites

The study was conducted in the framework of the EFForTS project (Georg-August-Universität Göttingen 2019), investigating ecological and socioeconomic changes associated with the transformation of lowland rainforest into agricultural systems (Drescher et al. 2016). Four land-use systems, rainforest (forest, F), jungle rubber agroforest (J), rubber monoculture (R), and oil palm monoculture (O; Fig. 1), were studied across two regions (Harapan and Bukit Duabelas landscape) in Jambi Province, Sumatra, Indonesia. Each system was investigated in eight replicate plots, four in each of the two landscapes, resulting in a total of 32 plots of 50 × 50 m with five 5 × 5 m subplots randomly placed per plot. Forests were classified as primary degraded rainforest (Margono et al. 2014), jungle rubber sites originating from disturbed rainforests enriched with rubber trees (*Hevea brasiliensis*); rubber and oil palm (*Elaeis guineensis*) monocultures were 12–14 yr old at the time of sampling.

Soil and vegetation parameters

Characteristics of the litter and the vegetation were assessed on each sampling site (Appendix S1: Table S1). During a vegetation survey, conducted from February 2013 to August 2014, all trees with a diameter at breast height ≥10 cm within the entire 50 × 50 m plot area, were identified and counted. Understory plants were assessed in the five 5 × 5 m subplots (a, b, c, d, e) within each plot: all vascular plant individuals growing within the subplots were identified and measured (height). Based on these data, we calculated tree species richness (TreeRich) and tree density (TreeDen) as well as understory species richness (UnderRich), understory density (UnderDen), and average understory height (UnderHeight). For more information about the vegetation survey see Rembold et al. (2017).

Parameters of litter and soil were assessed in three subplots (a, b, c): litter pH (CaCl₂) was measured using a digital pH meter, litter nitrogen (N) concentration was

analyzed using an elemental analyzer, and amount of litter was determined gravimetrically (for details see Kraševska et al. 2015). Density of earthworms in the litter and in the upper 5 cm of soil was investigated in three subplots (a, b, c) in 2013 using heat extraction (for details, see Potapov et al. 2019).

Spider collection

Different parts of the spider community were assessed in two separate sampling campaigns. The first campaign (litter sieving, LS) was conducted in October–November 2012 (Barnes et al. 2014). In three subplots per plot (a, b, c), the litter from a 1 × 1 m area was sieved through a 2-cm mesh sieve. All spiders visible by eye were hand-collected from the siftings and stored in 65% ethanol. The method represents large and mobile spider species. A total of 1,081 individuals were collected (Data S1: CommunityMatrix_spiders). The second campaign (heat extraction, HE) was conducted in October–November 2013 (Klarner et al. 2017). On each plot, the same subplots (a, b, c) were sampled with a spade. One soil sample of 16 × 16 cm was taken on each subplot, comprising the litter layer and the underlying mineral soil to the depth of 5 cm. Soil and litter from the second sampling campaign were transported in individual plastic containers and processed separately, but data were pooled for statistical analyses (but see Appendix S2). Spiders were extracted by heat (Kempson et al. 1963), collected in a dimethyleneglycol-water solution (1:1), and thereafter transferred into 70% ethanol. The method represents small and cryptic spider species. A total of 331 individuals were collected (Data S1: CommunityMatrix_HEspiders).

Spider identification

All adult spiders (43% of all individuals) were identified to (morpho)species using a Leica M125 (Leica Microsystems, Wetzlar, Germany) dissecting microscope and available identification keys for spiders in Asia, i.e., Barrion et al. (1995), Deeleman-Reinhold (2001), and Jocqué and Dippenaar-Schoeman (2006). In total, 139 species from 33 families were identified with 131 species found in the litter-sieving samples and 30 species in the heat-extracted samples with an overlap of 22 species between the methods (Appendix S2: Fig. S1). Species coverage (proportion of the collected species in the regional gamma diversity) was estimated as 41–80% in the litter-sieving samples and 60–86% in the heat-extracted samples based on four different criteria (Oksanen et al., 2011; Appendix S2: Fig. S2). Species coverage (proportion of the collected species in the Chao-based rarefied diversity) in individual sampling plots was estimated as 54% ± 23% in the LS and 72% ± 24% in the HE using *chao1* in the *rareNMtests* package in R 3.4.0 (R Core Team 2017; Appendix S2: Table S1). There were six sampling plots without identified species (i.e., adult

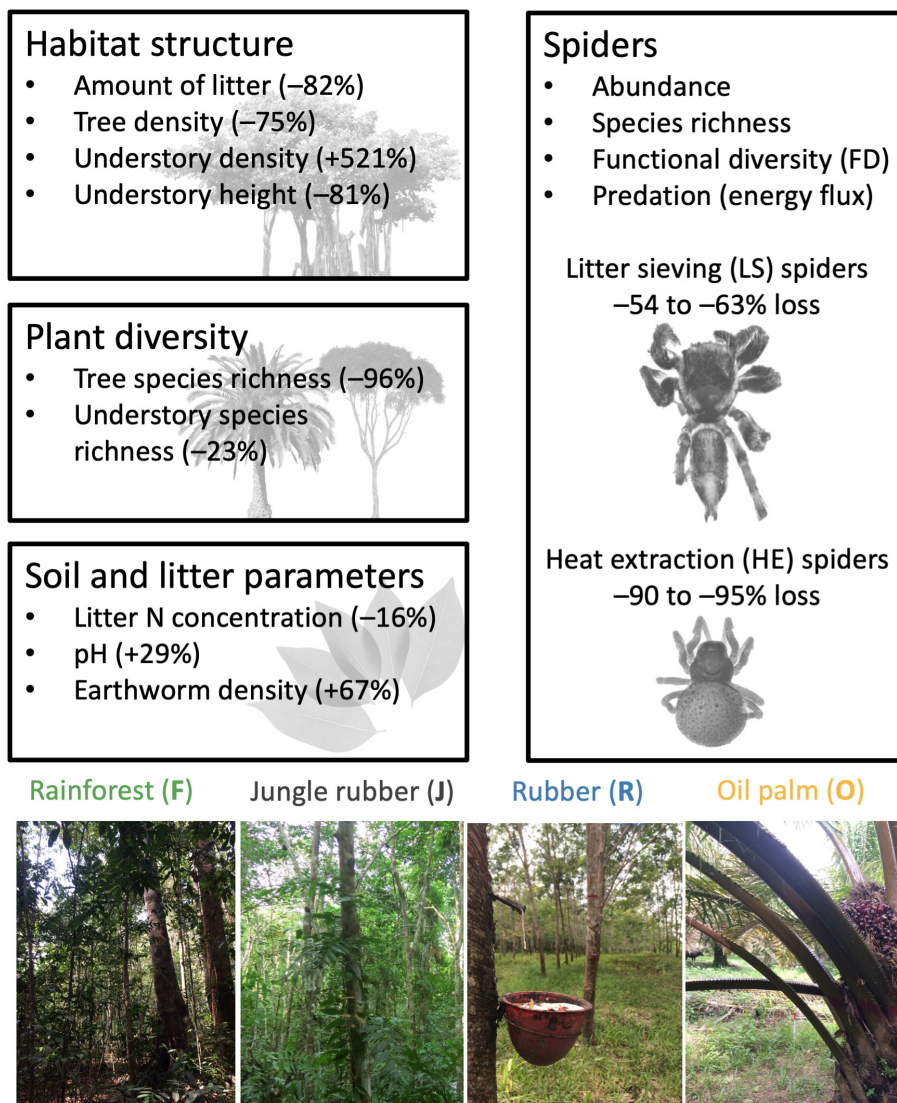


FIG. 1. Overview of the four land-use systems and parameters of litter, vegetation, and spider communities investigated. Soil-associated spiders were represented predominantly by the small cryptic species (e.g., Anapidae, lower spider), while LS spiders were represented predominantly by the larger mobile species (e.g., Salticidae, upper spider). Changes in all parameters from rainforest to oil palm monoculture are given in percent. Photo credits of jungle rubber, Jochen Drescher.

specimens) in the HE collection and one sampling plot without any spiders; there was one sampling plot without identified species in the LS collection. Samples with zero data were included in all analyses and calculations.

Imaging of representative specimens for each species was achieved using a custom-built BK Plus Lab System (Dun, Inc., USA) with integrated Canon EOS (Canon, Ōta, Tokyo, Japan) camera, macro lenses (65 mm and 100 mm), the stacking software Zerene Stacker (Zerene Systems, Richland, WA, USA) and formatted in Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, USA). All species and images are deposited in the Ecotaxonomy database (*available online*).¹⁵

¹⁵ <http://ecotaxonomy.org>

Calculation of energy flux to spider communities

To calculate the flux of energy from prey to spiders, as a proxy of community predation, we first estimated fresh body mass for each individual by measuring the body length (excluding appendages) and used it in a set of body-length–body-mass power equations (Höfer and Ott 2009). Second, we calculated metabolic rates from individual body masses (Ehnes et al. 2011) and then corrected them for assimilation efficiencies during transfer of energy between trophic levels (Barnes et al. 2014, 2018). Total flux to spider communities (i.e., predation) was calculated by summing up individual assimilation-corrected metabolic rates and expressed in kilograms fresh mass per hectare per year by assuming 1 kg fresh

mass = 7×10^6 J (Peters 1983). Calculations included juvenile spiders; more details on body mass and energy flux calculations are given in Appendix S3.

Assignment of traits and functional indices

In order to track differences in functional diversity and functional composition between spider communities in forest vs. other land-use systems, we choose functional traits (Violle et al. 2007) that are of high relevance for hunting and survival, and that could be inferred from the collected material considering poor knowledge on the biology of Indonesian spiders. Traits were assigned at the species level to each of the 139 collected spider species; since many species were identified as morphospecies (i.e., potentially undescribed species; Appendix S1: Table S2), some trait categories were extrapolated from corresponding families. Five trait dimensions were distinguished, each reflecting different aspects of spider predation (effect traits), and also responses to environmental/ biotic alterations (response traits):

- 1) *Hunting strategy*, reflecting how spiders hunt prey. Six categories were distinguished (Wise 1995, Jocqué and Dippenaar-Schoeman 2006, Herberstein 2011): free hunters, ant mimickers, and four types of web builders (orb-type, sheet-type, cob-type and silk-line burrow). Spiders with different hunting strategies vary in the success of catching prey differing in behavior and mobility (Ludwig et al. 2018).
- 2) *Body coloration*, reflecting the importance of visual characters in communication with the biotic environment. Since coloration often functions to improve camouflage (Oxford and Gillespie 1998), spiders with different coloration are likely to be confined to certain microhabitats. Five categories were distinguished: patterned coloration (clear pattern of spots or stripes on the body), dark coloration (clearly pronounced, but uniform coloration), and pale coloration with full eyes, reduced eyes, and absent eyes.
- 3) *Habitat*, representing the general spatial niche of species, primarily corresponding to vertical stratification. Five categories were distinguished (Jocqué and Dippenaar-Schoeman 2006): arboreal (living on aboveground parts of plants), arbustive (living on vegetation close to the ground), ground (living on surface of the litter), cryptic (living within the litter/ soil or using other shelters), and generalist (highly mobile species that are not restricted to a single habitat).
- 4) *Desiccation resistance*, reflecting the ability to remain active in dry habitats or seasons mediated by abdominal scuta (Main 1976). Since the species with scuta are likely able to endure dryer conditions, we presume that they may hunt in dry periods or in drier microhabitats. Two categories were distinguished: presence or absence of scuta.
- 5.. *Body mass*, reflecting the ability to handle prey of different size (Brose et al. 2019), the resource requirements of the organism (Turney and Buddle 2019), and also dispersal ability, which is important for being able to colonize systems after land-use change. Five size classes based on \log_{10} -scaled fresh body mass were distinguished: <0.1 mg, 0.1–1 mg, 1–10 mg, 10–100 mg, and >100 mg.

Five trait dimensions well separated the morphospecies, in total 60 trait combinations were found (Appendix S1: Fig. S1). The matrix of species' traits was transformed into a dendrogram using first *daisy* (Gower's distances for nominal variables with log-transformed body size taken as a numeric variable) and then *hclust* in R. Dendrogram was used to calculate functional diversity (FD) in each spider community (i.e., plot) using *treediv* in the *vegan* package. Functional diversity in this case was calculated as the total branch length among species present in the local community on the trait dendrogram (Petchey and Gaston 2002).

Statistical analysis

All calculations were done in R 3.5.3 with R studio interface 1.0.143 (RStudio, Inc., Boston, MA, USA). Since LS and HE sampling events were performed in different years, utilized different sampling areas and covered different parts of spider community (Appendix S2), we present the two sampling methods separately along with the combined data set. In the analyses, sampling plots were treated as replicates ($N = 32$). Effects of land use (F, J, R, O) and region (Harapan or Bukit Duabelas) were evaluated in a series of generalized linear models (*glm*); model choice followed the distribution of response variables and visual inspection of residuals. We first used Poisson distribution for the count data and Gaussian distribution for other data. Data on understory density were \log_{10} -transformed prior to analysis, which improved homogeneity of variance. Among the parameters of litter and vegetation, earthworm abundance, tree species richness, tree density, and understory species richness were analyzed as count data. Effects of land-use system and region on spider abundance (number of collected individuals per plot, including juveniles), species richness (number of collected species per plot), and number of species with specific traits (count data) were also analyzed as count data. We tested for overdispersion in all Poisson models with *dispersiontest* in the *AER* package. In all cases except for species richness of HE spiders, the models were overdispersed and so we remodeled overdispersed data on a negative binomial distribution (*glm.nb*). Effects of land-use system on energy flux to spider communities (including juveniles) and FD were analyzed using a Gaussian distribution. Differences between means were inspected using post hoc Tukey's HSD test for multiple comparisons with *glth* in the

multcomp package (Hothorn et al. 2008). The model results are given in Appendix S1: Tables S3–S5.

Further, we studied how parameters of litter and vegetation affect parameters of spider communities independent of land-use system and region. Due to a high number of parameters to avoid multicollinearity, we grouped all parameters in (1) habitat structure parameters (TreeDen, UnderDen, UnderHeight, and amount of litter), (2) plant diversity parameters (TreeRich and UnderRich), (3) other soil and litter parameters (litter pH, litter N concentration, and earthworm abundance). Further, principal component analysis was applied using *prcomp* to each group separately. For habitat structure parameters PC1 explained 73.5% of the variation and was positively correlated with UnderDen and negatively with other factors, PC2 explained 12.9% of the variation and was positively correlated with UnderDen and UnderHeight, PC3 explained 9.8% of the variation and was positively correlated with TreeDen and negatively with amount of litter. For plant diversity parameters, PC1 explained 97.0% of the variation and was negatively correlated with TreeRich and UnderRich (Appendix S1: Tables S6, S7). Other soil and litter parameters were poorly intercorrelated so we did not use principal components for them. The most parsimonious model explaining the abundance, species richness, FD and energy flux of spider communities was selected by comparing a set of models using AIC (Akaike Information Criterion). Due to collinearity of habitat structure and plant diversity, first these two groups of factors (i.e., their principal components) were compared. Further, a more parsimonious model was complemented by either pH, litter N concentration, earthworm density, or all these factors together, and the final model was selected. The model results are given in Appendix S1: Tables S8, S9.

To compare the rate of species and trait change, we calculated dissimilarity of species and trait combinations among four land-use systems (plots in each system were merged together) using *beta.multi* in the *betapart* package. The function estimates overall beta diversity (Sørensen dissimilarity) and partitions it into nestedness (loss of species or trait combination) and turnover components (replacement of species or trait combinations; Baselga 2010). To test the difference in the rate of species and trait change, we analyzed number of species and number of trait combinations in a single variable number of forest species/traits. To do that, we selected only species and trait combinations that were found in rainforest. Thereafter, effects of interactions between land-use system and parameter type (species or trait combinations) on the number of forest species/traits were evaluated using generalized linear models (Poisson distribution). In this case, a significant interaction between the effect of parameter type and respective land-use system indicates a different magnitude in the change in rainforest species and rainforest trait combinations and, thus, significant differences in species and trait loss/gain from

rainforest to the respective land-use system. Significance was evaluated using *Anova* in the *car* package.

Due to low number or absence of species collected by HE in some plots in oil palm monocultures, community composition of HE spiders could not be analyzed separately from LS spiders and we combined both methods. Since density estimations differed strongly between the two sampling methods (see Appendix S2), we used proportions of species in total number of identified individuals for each community instead of using raw count data or density estimations. A community matrix with proportions of species or traits, averaged for the two methods, was used in nonmetric multidimensional scaling (NMDS) using *metaMDS* based on Bray-Curtis dissimilarities in the package *vegan* (Oksanen et al., 2011) to illustrate differences in species and trait compositions among land-use systems. Two dimensions were used for NMDS, plots were treated as replicates, and only species present on more than one plot were analyzed. For the trait composition analysis, we used counts of specific trait categories (see above); spiders with fresh body mass >50 mg were classified as “large” while those with fresh body mass <0.1 mg were classified as “small.” Proportions of traits were calculated using the number of identified individuals per plot as total. Litter and vegetation parameters were fitted in the scaling space to illustrate their effect on the distribution of traits and species; data on understory density were log₁₀-transformed prior to the analysis. Using binary data or proportion of species in the overall maximum instead of proportions of species in the total for each community changed the scale, but showed similar dissimilarity between land-use systems with the same factors being significant (data not shown). Differences between land-use systems were tested using analysis of similarities based on species/trait proportions (*anosim* in package *vegan*). Data are presented as means ± SD, with *P* < 0.05 taken as the level of significance.

RESULTS

Spider density, energy flux, and diversity

Despite a lower number of sampled species and individuals, the density of HE spiders was one order of magnitude higher than the density of LS spiders (Fig. 1; Appendix S2). Spider density and energy flux per unit area for spiders collected by both HE and LS were generally reduced in plantations as compared to rainforest and this was most prominent in oil palm monoculture (Fig. 1; Appendix S1: Table S10). The reduction was much more pronounced for the density of HE spiders, which decreased by 90% from rainforest to oil palm monoculture. Compared to rainforest ($112 \pm 59 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), energy flux in the spider community collected by HE was reduced in jungle rubber by 72%, in rubber monoculture by 55%, and in oil palm monoculture by 94%. Energy flux in LS spiders was

$20 \pm 7 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in rainforest and was reduced by 57% only in oil palm monoculture. In contrast to HE spiders, energy flux in the LS spider communities was similar in rainforest, jungle rubber, and rubber, whereas density was reduced by 30% and 55% in rubber and oil palm monocultures, respectively, as compared to rainforest (Fig. 1; Appendix S1: Table S10).

Spider species richness and functional diversity per plot were significantly reduced in oil palm monoculture as compared to rainforest. The loss in species richness, rarefied richness, and FD per unit area in HE spiders was about 75–80% in jungle rubber and rubber monoculture, and about 91–98% in oil palm monoculture. The loss in these parameters in LS spiders was small in jungle rubber and rubber monoculture, but was 57–63% in oil palm monoculture (Fig. 2; Appendix S1: Table S10). The overall loss in species richness when both sampling methods were combined comprised about 30% in jungle rubber and rubber monoculture and 67% in oil palm monoculture as compared to rainforest. Corresponding losses in FD were slightly less pronounced (20% and 60%, respectively; Fig. 2). Functional redundancy (estimated as the ratio between species richness and FD) was similar in HE spiders and in LS spiders in rainforest (1.76 ± 0.33 and 1.68 ± 0.32 , respectively). Species richness and FD were intercorrelated across land-use systems, but the slope was steeper in plantation systems, suggesting lower functional redundancy when compared to rainforest communities. This was consistent in spider communities collected by HE, LS, and both methods combined (Fig. 2).

All studied parameters of vegetation and soil except for understory density, pH and earthworm density were negatively affected by the land-use change from rainforest to monocultures. Understory density was five times higher in oil palm monoculture than in rainforest, while pH and earthworm abundance were increased by 29% and 67%, respectively (Fig. 1; Appendix S1: Table S10).

The most parsimonious model explaining variation in abundance, species richness, and FD for both HE and LS spiders included only principle components of habitat structure. In all cases, these spider community parameters were negatively related to PC1 (i.e., a positive effect of the amount of litter, tree density, and understory height) and to PC3 (i.e., a positive effect of the amount of litter, but a negative effect of tree density), but were positively related to PC2 (i.e., a positive effect of understory density and height). The effects were similar in magnitude, but the effect of PC1 was more statistically clear (lower P values) in the majority of cases. The effect of PC4 was weak and not significant. Abundance of HE spiders was also negatively affected by earthworm abundance, although this effect was small. In contrast to abundance and diversity, predation (energy flux) of HE and LS spiders was better explained by PC1 of plant diversity (a positive effect of tree and understory species richness), but the effect was not significant for LS spiders (Appendix S1: Tables S8, S9).

Turnover and loss of species and traits

Dissimilarity of species among land-use systems (71% for HE, 82% for LS, and 78% for HE and LS combined) was higher than dissimilarity of trait combinations (64% for HE, 60% for LS, and 57% for HE and LS combined). For LS spiders and the combined data set, the turnover component of dissimilarity was higher for species (79% and 74%, respectively) than for trait combinations (54% and 49%, respectively). By contrast, these community attributes were more similar for HE spiders (52% for species and 48% for traits). The nestedness component of dissimilarity in LS spiders and combined data set overall was small, but higher for trait combinations than for species. Nestedness in HE spiders was 19% for species and 15% for trait combinations (Fig. 3).

Species and functional trait loss occurred at similar rates in HE spider communities (Fig. 3b). In oil palm plantations, no rainforest species and functional trait combinations were found and they were barely replaced by new species/combinations. In LS spider communities, species loss was significantly stronger than functional trait loss in rubber and oil palm monoculture ($\chi^2_3 = 14.8$, $P = 0.0020$; Appendix S1: Table S11; Fig. 3c). Despite very few rainforest species appearing in plantations, the loss of functional trait combinations was less pronounced due to other colonizing species with similar functional trait combinations.

Species composition in the combined HE and LS data set differed clearly between more natural (rainforest and jungle rubber) and more intensified systems (rubber and oil palm monocultures; anosim $R = 0.42$, $P < 0.001$). The difference in taxonomic composition was visible at the level of families (see Appendix S4: Fig. S1) and clearly pronounced at the level of species (Fig. 4a); 26 species were found only in rainforest, while 82 species were found only in plantation systems. Most of the measured environmental factors contributed to distinction between rainforest/jungle rubber and monocultures, while differences within these groups were not related to measured factors (Fig. 4a).

Trait composition differed much less than species composition among land-use systems (anosim $R = 0.17$, $P = 0.015$). Monocultures were characterized by a higher number of generalists, species with patterned coloration, and cob-web building species, while rainforest was characterized by species of small size, orb-web builders, species covered with scutum, and species living in cryptic habitats (Appendix S4: Table S1). Difference in trait composition was related primarily to the amount of litter, understory density and height, and pH (Fig. 4b).

DISCUSSION

We found declines in abundance and biomass and strong shifts in the composition of species and functional traits of spider communities with land-use change

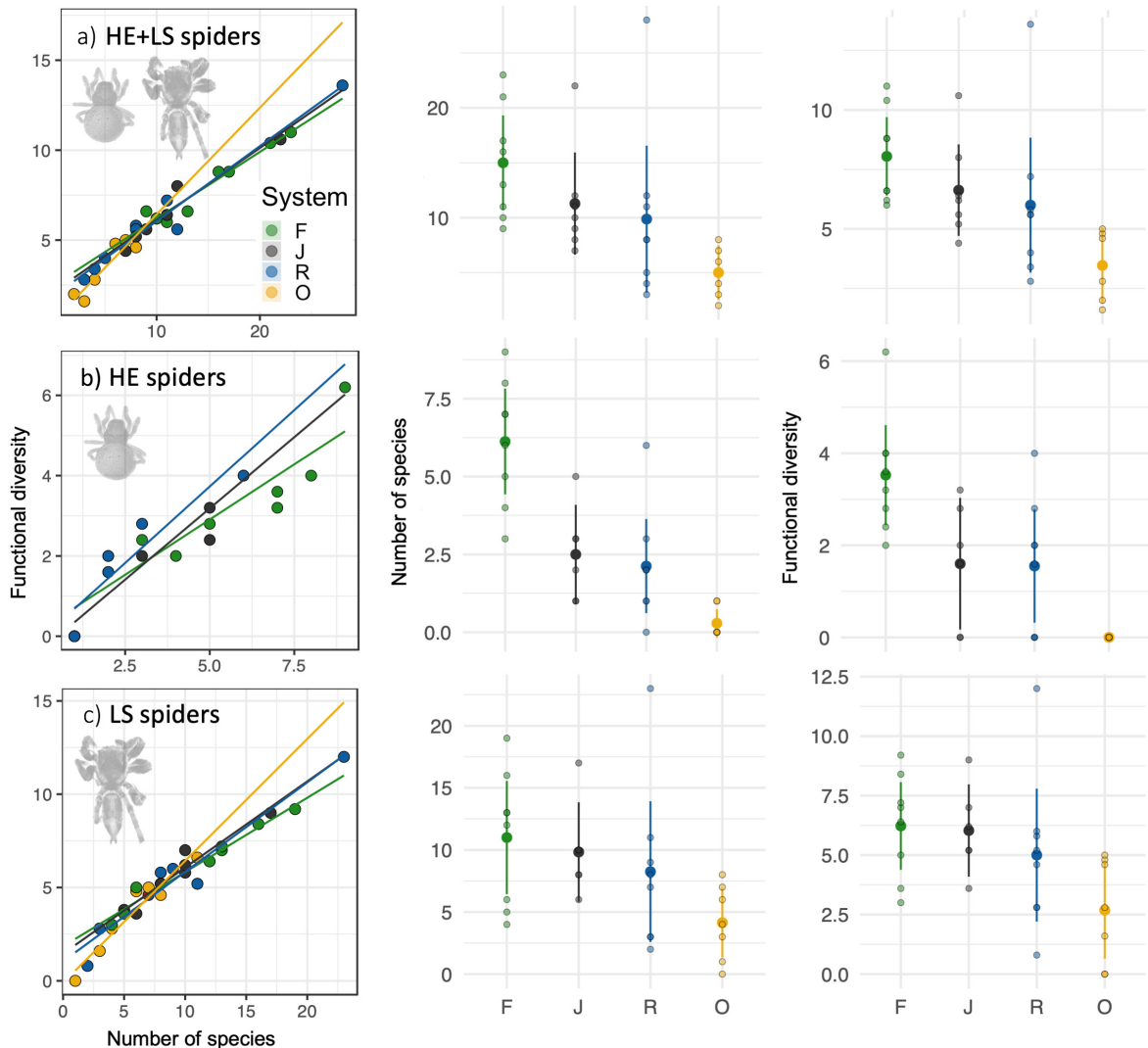


FIG. 2. Species richness and functional diversity in spider communities across the studied land-use systems. In rows: (a) HE and LS spiders combined, (b) HE spiders, and (c) LS spiders. In columns, from left to the right: (1) correlation between species richness and FD values (functional diversity as the total branch length on dendrogram) in spider communities across the studied land-use systems; (2) number of species in each land-use system, means and 95% confidence intervals; (3) FD values in each land-use system, means and 95% confidence intervals. Each point represents a plot, land-use types are shown in different color: rainforest (F, green), jungle rubber (J, gray), rubber monoculture (R, blue), and oil palm monoculture (O, yellow). FD of HE spiders in oil palm monoculture is not shown since communities comprised only one, if any, identified species in most of the cases.

from rainforest to oil palm monoculture. Land-use change was associated with an almost complete species loss and turnover in the spider communities. However, the species turnover did not compensate for the loss of many functional trait combinations. Community energy flux was reduced by up to 94% in spiders collected by heat extraction (HE) and up to 57% in spiders collected by litter sieving (LS) in monoculture plantations, suggesting a strong reduction in predation pressure by ground-associated spiders in comparison to rainforests. These changes were explained the best by habitat structure degradation and change and occurred irrespectively of the collection method.

The differences between the two collection methods emphasize that small cryptic spiders, collected by HE, already respond to moderate habitat changes such as conversion of rainforest into jungle rubber, while larger LS spiders retain higher diversity and biomass in rainforest, jungle rubber, and rubber monoculture. Turnover of species was attributed to the loss of small species, orb-weaver builders, species with scutum, and species living in cryptic habitats, and the gain of generalists, species with patterned coloration, and cob-web builders. The stronger decline in the small species was surprising as larger species are often found to react more strongly to disturbances and land-use change (Brose et al. 2017).

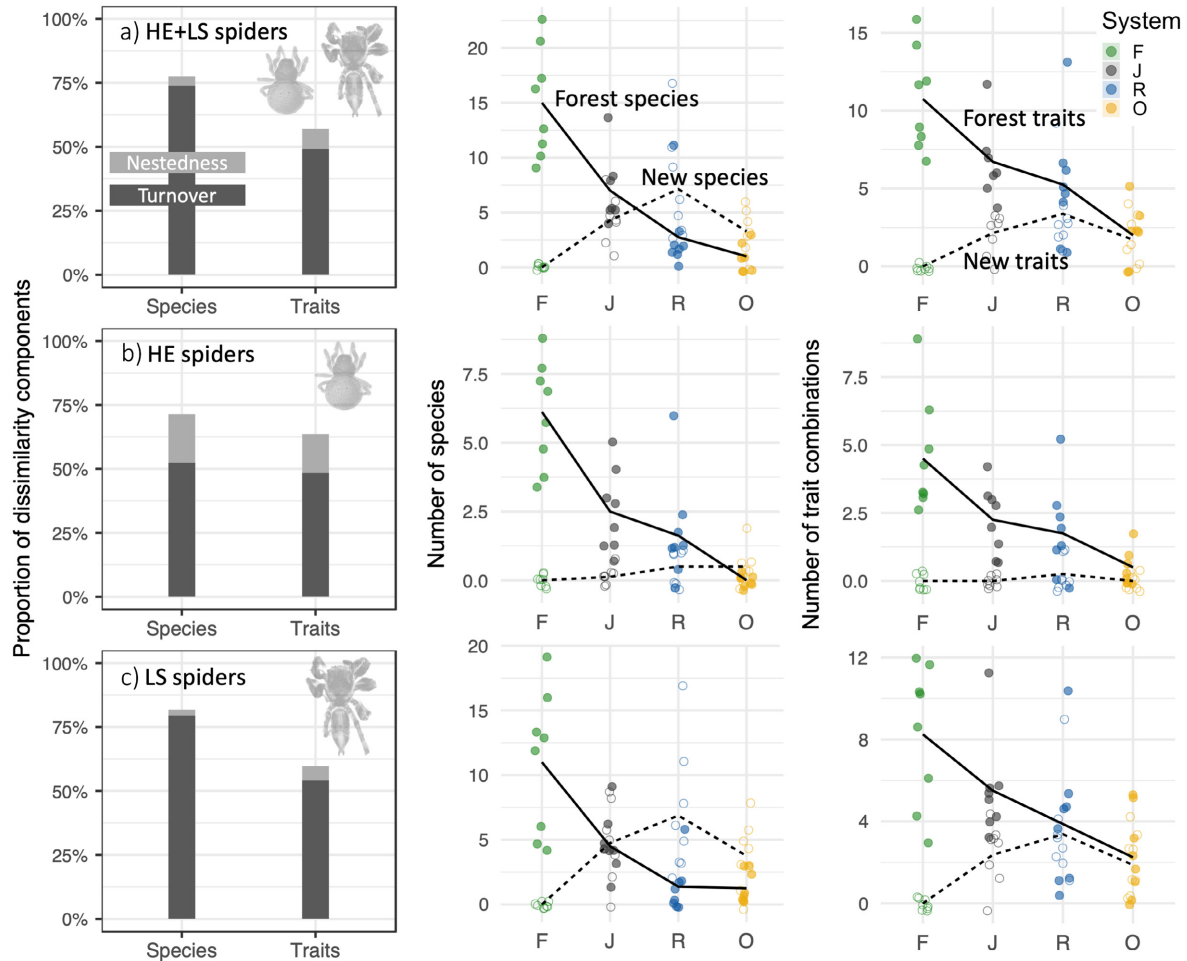


Fig. 3. Spider trait and species turnover with land-use change. In rows: (a) HE and LS spiders combined, (b) HE spiders, and (c) LS spiders. In columns, from left to the right: (1) nestedness and turnover components of Sorensen dissimilarity of species and trait combinations among all land-use systems; (2) changes in the number of species present or absent in rainforest, lines connect mean values; (3) changes in the number of trait combinations present or absent in rainforest, lines connect mean values. Each point represents a plot, land-use types are shown in different color: rainforest (F, green), jungle rubber (J, gray), rubber monoculture (R, blue) and oil palm monoculture (O, yellow). Loss of forest trait combinations is significantly slower than loss of forest species in LS spider communities (Appendix S1: Table S8).

Predation loss in litter and soil

The magnitude of land-use-driven community change differed strongly between soil-associated and litter-associated spider communities. Different sampling methods often provide information on different aspects of tropical litter and soil invertebrate communities (Sakchoowong et al. 2007), and thus a combination of methods provides better understanding of community changes. As the samples of both methods were taken at the same time of the year, the very pronounced differences in density and taxonomic composition presumably reflect that the two methods represent very different fractions of spider communities, thereby being complementary (Appendix S2). HE favored catches of small cryptic species, predominantly of the family Oonopidae,

dwelling in the litter and upper soil layer (hereafter “soil-associated”). LS favored catches of larger mobile species of various families living mainly in the litter, on the litter surface and on understory vegetation above the litter (hereafter “litter-associated”).

The density and total predation per unit area (energy flux) of soil-associated spiders exceeded that of litter-associated spiders by up to an order of magnitude. Moreover, the data suggest that, except in rainforest, the density of spiders in the top 5 cm of soil markedly exceeds that in litter (Appendix S2), suggesting that tropical lowland ecosystems are characterized by a large number of small cryptic soil spiders. In part, this was due to a high incidence of juveniles among soil-associated spiders (64% of total), but the fraction of juveniles in litter-associated spiders was only slightly lower (52%).

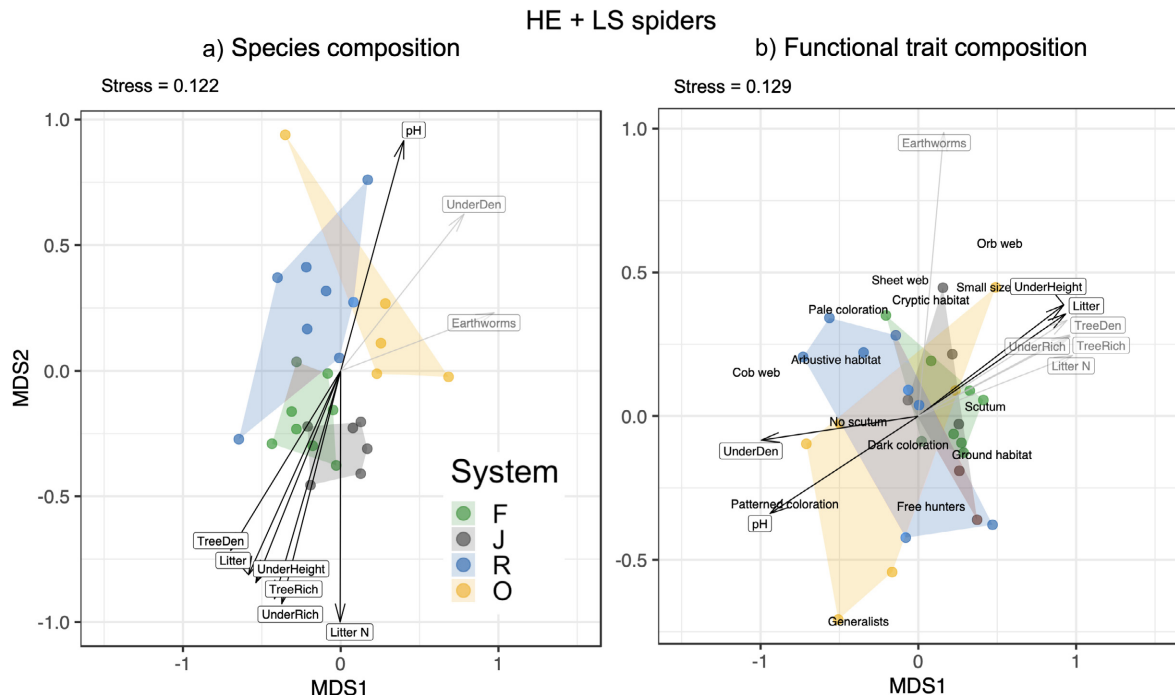


FIG. 4. Differences in species and trait composition between land-use systems illustrated with multidimensional scaling. Land-use types are shown in different color: rainforest (F, green), jungle rubber (J, gray), rubber monoculture (R, blue), and oil palm monoculture (O, yellow). Each point represents one plot; text in panel b represents traits. Combined data of HE and LS are presented. Only species present on more than one plot were analyzed. Litter and vegetation parameters that statistically clear affected the distribution of traits and species are shown with black arrows and labels; other included parameters are shown in gray. Parameters are tree species richness (TreeRich), tree density (TreeDen), understory species richness (UnderRich), understory density (UnderDen), average understory height (UnderHeight), amount of litter (Litter), litter nitrogen concentration (Litter N), abundance of earthworms (Earthworms), and pH.

Although only few spider species were extracted exclusively from soil, the results suggest that total density and predation by spiders is strongly underestimated if soil-dwelling species are ignored.

In rainforest, the overall predation by soil-associated spiders exceeded that by litter-associated spiders by a factor of five. By contrast, the overall predation rates were similar between the two methods in oil palm monoculture due to the strong decline in abundance of soil-associated spiders. Despite the different responses, the decline in both groups was primarily related to the changes in habitat structure, such as understory density and height and reduction of the litter layer in oil palm monoculture. The effect was stronger for small cryptic soil-associated spiders, suggesting that they predominantly suffer from the loss of litter shelter. A positive effect of understory density and height on density and diversity of soil-associated and litter-associated spiders supports other studies showing that complex ground vegetation promotes ground invertebrate communities in plantations (Ashton-Butt et al. 2018). Unlike taxonomic and functional diversity, predation by spiders was affected rather by plant diversity than habitat structure. These results suggest that enhancing both diversity and habitat structure in plantation monocultures may be the

most promising approach to maintain natural biological control provided by functionally diverse spider communities. As plant diversity increase structural complexity in plantations, maximizing both may be possible with little additional efforts (Zemp et al. 2019).

Heat extraction allowed us to show the strong reduction in density and energy flux of the small spider species in jungle rubber, i.e., agroforest systems of moderate land-use intensity. As suggested by our model, the decline in density of soil-associated spiders might in part be related to invasion by earthworms, with their biomass being 60–100 times higher in plantation systems and jungle rubber as compared to rainforest (Potapov et al. 2019). Earthworms may directly consume small soil invertebrates including hatchlings and eggs of spiders (Curry and Schmidt 2007) or disrupt their webs. By contrast, the moderate effect of land use on the large litter-dwelling and arbustive litter-associated spider species suggests that these spiders are less tightly linked to small soil prey or more easily switch to alternative prey such as aboveground invertebrates (Scheu 2001). The observed shift in the relative importance of the flux of energy through soil-associated and litter-associated spider communities suggests principally different pathways of energy flux through food webs of rainforest and

agricultural land-use systems. Combined data suggest that land-use systems such as jungle rubber and rubber monoculture sustain a high functional diversity of ground spiders, but negatively affect predation of small cryptic species. By contrast, oil palm monoculture sustains only limited functional diversity and predation by spider communities.

Rate of species and functional trait loss

The overall decline in species richness and functional diversity of spider communities in this study is in accordance with observations on the entire litter and soil invertebrate communities (Barnes et al. 2014, Mumme et al. 2015, Potapov et al. 2019). The two sampling methods used in our study demonstrated two different aspects of community responses to land-use change. The soil-associated spider community responded much stronger and the loss of species occurred at the same rate as the loss of functional trait combinations. Density, biomass and energy flux per unit area declined by more than 90%. These strong changes led to a simultaneous loss of sets of redundant species and new communities assembled including few species with new functional trait combinations. By contrast, changes in the litter-associated spider community were less pronounced with the loss of species exceeding the loss of functional trait combinations; 10–17% of forest species, but 31–48% of forest trait combinations, were found in monoculture plantations. We also found a large overlap in trait, but not species composition, between land-use systems. The stronger reduction in species richness as compared to functional group richness is in line with that of the entire litter invertebrate community (Mumme et al. 2015). Since functional redundancy was similar in soil-associated and litter-associated spiders in rainforest, it is likely that the loss of species and functional traits with rainforest conversion was related to the magnitude of disturbance (land-use change more strongly affected soil-associated spiders). The litter-associated spider community was only moderately affected by land-use change and the overall set of functional trait combinations changed slowly due to colonization by new species with similar functional traits as in rainforest species, but presumably coping better with the new environment than rainforest species (Appendix S4: Fig. S2). As a result, overall species richness and functional diversity changed little, except in oil palm monoculture.

Changes in community composition

Land-use change from rainforest to monoculture plantation systems was associated with an almost complete species loss and turnover in the spider communities with <20% of rainforest species being present in rubber and oil palm monocultures, irrespective of the collection method. This is in line with previous studies on prokaryotes, testate amoebae, and plants from the same

sampling sites that reported major community shifts from rainforest to plantation systems (Schneider et al. 2015, Krashevska et al. 2016, Rembold et al. 2017). The turnover component (replacement of species) overall strongly exceeded nestedness of communities across land-use systems. Nestedness was higher in soil-associated communities, which, together with a strong decline in diversity, suggests that land-use change from rainforest to monocultures does not open new ecological niches for small cryptic species. Turnover was the main pattern in litter-associated spider communities. We found 82 species exclusively in plantation systems, suggesting a large potential of either external colonization (dispersal from other habitats to deforested area) or “internal resilience” (reproduction of rare species, that were present in the community before deforestation).

Trait composition of spider communities was affected by habitat-structural parameters such as density of understory, understory plant height, and the amount of litter. This may reflect a strong link between functional composition of arthropod community and the structural complexity and structural characteristics of habitats (Lassau et al. 2005). In particular, the amount of litter in rubber, and especially in oil palm plantations, is lower than in rainforest (Krashevska et al. 2015). Species of the families Oonopidae and Tetrablemmidae; i.e., small spiders using leaf litter as shelter and for hunting (Jocqué and Dippenaar-Schoeman 2006), suffered the most (Appendix S4). The absence of litter in oil palm plantations also affects the composition of other ground arthropods such as beetles (Chung et al. 2000). The reduction in leaf litter may also explain the absence of spiders with reduced vision, and the reduction in ground, cryptic and small-sized species dwelling in shelters. The increase in understory plant density may explain the presence of arbustive species and species implying three-dimensional cob webs. Patterned coloration occurred more frequently in monoculture plantations, suggesting that in more open habitats visual cues are more important and favor mobile, visual-hunting, predator species. Thus, the structural components of habitat are likely to support the diversity and shape the composition of functional traits in communities of ground-associated invertebrate predators.

CONCLUSIONS

Our study is the first to use a trait-based approach for analyzing tropical spider communities to understand the drivers of community turnover and invertebrate predation loss with land-use change. Conversion of rainforest to monoculture systems strongly affected ground spider communities, resulting in the loss of diversity and ecosystem functions they provide; total predation, estimated as energy flux to spiders, was reduced by 94% and 57% in oil palm monoculture for both soil-associated and litter-associated spider communities, respectively. Land-use systems such as jungle rubber and rubber monocultures

sustain a high functional diversity of mobile litter-dwelling and arbustive spiders, but negatively affect predation of small cryptic species. Oil palm monocultures sustain only limited functional diversity and predation by spider communities. Small cryptic spiders, which are often ignored in ecological studies, form an important component of spider communities in tropical rainforests, but are less abundant in plantation systems.

Plantation systems are colonized by many spider species, in part replacing species being excluded, but this turnover does not compensate the losses in functional diversity and predation per unit area. The ratio of species-to-trait losses and loss of functions likely depend on the magnitude of disturbance, with moderate changes allowing for colonization of new species that play similar functional roles as the species being lost, which gives some promise for potential conservation practices. Functional diversity and composition were primarily related to the structural complexity of the habitat, specifically to the amount of litter and ground vegetation density and height, while predation by spiders was related to plant diversity. Thus, the negative impacts of land-use change on spider communities might be mitigated by adopting management strategies such as mulching and reduced weeding/herbicide application (Ashton-Butt et al. 2018, Tao et al. 2018) or intercropping monocultures with other trees (Teuscher et al. 2016). Further, to improve colonization of monoculture plantations from refuge areas, our findings suggest that plantations are best integrated into complex landscapes comprising different habitat types including rainforest.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2957/supinfo>

DATA AVAILABILITY

Data are available on Figshare: <https://doi.org/10.6084/m9.figshare.10305506>